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Vegetation pattern along a topographical gradient in a beech forest reserve in the Mecsek Mts (Hungary)

Vegetationsmuster entlang eines topographischen Gradienten in einem Buchenwald-Reservat im Mecsek-Gebirge (Ungarn)

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Key words: Spatial heterogeneity, Gap, Transect, Boundary, Moving split window

Summary

Transitions between neighbouring vegetation units form one of the central issues in ecology. The topic is especially interesting in the case of natural or near-natural forests, where different forest types are arranged along gradients, interspersed with gaps. In this article, our aim was to identify the spatial sequence of forest types along a topographical gradient in a forest reserve in the Mecsek Mts, Hungary. We wanted to charaterize the sharpness of the boundaries between adjacent units, as well as to describe the different segments identified. A belt transect, running from a beech forest into a turkey oak-sessile oak forest, was established. The transect consisted of 376 plots, 2 m^2 each. Presence of all vascular plant species of the herb layer was registered in each plot along the transect. Vegetation boundaries

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were delineated both visually (during field works) and objectively (using the multivariate moving split windows – MSW – technique). The segments were compared based on physiognomy, species richness, ecological indicator values, geoelement spectra and species' coenological preferences. We identified eight segments visually, all of which could be verified by the MSW analysis. The high peaks indicated sharp boundaries, reflecting sudden compositional changes due partly to physiognomic changes, partly to the steep topographical gradient. MSW peaks were shifted to the north in each case, compared to the visual boundaries, the average spatial difference being 6.14 m. This is consistent with earlier studies on the light regime of the northern edges of the gaps. Forest gaps as well as the xeric end of the transect proved to be more species rich than the other segments. In contrast, ecological indicator values, geoelement spectra and species' coenological preferences did not show marked gap vs. closed forest differences; instead, there were gradual trends in these characteristics from the valley bottom to the valley edge. Thus, the strong topographical gradient had a much larger influence on these features than canopy openness. We hope that our study contributes to a better understanding of the spatial heterogeneity of near-natural beech and oak forests, and it may serve as a starting point for monitoring surveys in the forest reserve of the Mecsek Mts.

Zusammenfassung

Räumliche Übergänge zwischen benachbarten Vegetationseinheiten gehören zu den zentralen Themen in Ökologie, die besonders interessant im Falle von natürlichen oder naturnahen Wäldern sind, wo verschiedene Waldtypen und verstreute Lichtungen entlang Gradienten aufzufinden sind. In diesem Artikel wollten wir die räumliche Sequenz der Waldtypen entlang eines Gradienten in einem Buchenwald-Reservat im Mecsek-Gebirge (Ungarn) feststellen. Unser Ziel war die Schärfe der Grenzen zwischen benachbarten Einheiten zu characterisieren, sowie die verschiedenen Segmente zu beschreiben.

Ein Transekt wurde gegründet, der von einem Buchenwald bis einen Zerreichenwald erstreckte. Der Transekt bestand aus 376 Quadraten, je 2 m^2. Wir registrierten die Präsenz aller Gefäßpflanzen der Krautschicht in jedem Quadrat entlang der Transekt. Vegetationsgrenzen wurden sowohl visuell (während der Feldarbeiten) als auch objektiv (mit dem multivariablen moving split window – MSW – Technik) festgestellt. Die Segmente wurden auf Basis von Physiognomie, Artenreichtum, ökologische Zeigerwerte, Spektrum der Florenelementen und Spektrum der zönologischen Präferenzen verglichen. Acht Segmente wurden visuell festgestellt, und alle wurden durch die MSW-Methode bestätigt. Die hohen Spitzen deuteten auf scharfe

Grenzen, die plötzliche Veränderungen in der Zusammensetzung der Arten markierten, zum Teil wegen der physiognomischen Veränderungen, zum Teil wegen der steilen topographischen Gefälle. Wenn mit den visuellen Grenzen verglichen, MSW-Spizten waren in jedem Fall nach Norden verschoben; die durchschnittliche Differenz war 6.14 m. Dies steht in Übereinstimmung mit früheren Studien über die Lichtverhältnisse im nördlichen Rand der Lichtungen. Lichtungen und die xerophile Ende des Transekts erwiesen sich mehr artenreich als die anderen Segmente. Ökologische Zeigerwerte, Spektrum der Florenelementen und Spektrum der zönologischen Präferenzen dagegen zeigten keine deutliche Unterschiede zwischen Wald und Lichtung; stattdessen gab es ein allmählicher Trend von der Talsohle zum Talrand. Die starke topographische Gefälle hatte einen viel größeren Einfluss auf diese Attribute als die Offenheit der Kronenschicht. Wir hoffen, dass unsere Studie zu einem besseren Verständnis der räumlichen Heterogenität der naturnahen Buchen-und Eichenwälder beitragen wird, und es kann auch als Ausgangspunkt für Monitoringsstudien in der Waldreservat des Mecsek-Gebirges dienen.

1. Introduction

The arrangement of plant populations and communities along environmental gradients belongs to the central issues in vegetation ecology (cf. Gleason, 1926; Clements, 1936; Whittaker, 1967; Austin, 2005). The sharpness or vagueness of the transitions between neighbouring communities situated along a gradient is particularly interesting. Numerous studies have shown that in nature both sharp and blurred boundaries exist, and in some cases transitions are so gradual, that no boundaries can be delineated (e.g. Hobbs, 1986; Kirkman et al., 1998; Erdős et al., 2012). Major physiognomic differences (e.g. in the case of a forest-grassland boundary) often result in sharp compositional boundaries (e.g. Ludwig and Tongway, 1995; Hennenberg et al., 2005; Erdős et al., 2011; Dupuch and Fortin, 2013), although there are also contradicting results (e.g. Chabrerie et al., 2013).

The situation is more complicated if changes in vegetation structure are less conspicuous. Adjacent forest communities usually intergrade into one another more or less gradually, without any sharp boundaries. Ortmann-Ajkai (2002) demonstrated that coenologically typical oak-ash-elm and oak-hornbeam stands on a floodplain, along a weak altitude and groundwater level gradient, could not be separated clearly either by coenological or by multivariate analyses: there is a gradual transition zone of some hundred meters between them. Hrivnak et al. (2013) found a continuous unimodal distribution of species along an altitudinal gradient of Central European beech

forests in the herb, shrub and canopy layers each. Penksza et al. (1995) analysed a sequence of mesic forest communities along an altitudinal gradient. In the transect, the species of the canopy layer formed marked boundaries, but the herb layer showed a rather gradual spatial species turnover. Similarly, no significant boundaries were revealed among the herb layer communities of neighbouring mesic forest stands in the studies of Erdős et al. (2012, 2013a), which used the moving split window (MSW) analysis for boundary detection. However, there are some researches showing entirely different results. Pärn et al. (2010) were able to delineate well-defined boundaries in the herb layer along a transect that crossed different forest types growing on different soils. Also, the results of Bátori et al. (2014) indicate that boundaries between mesic forests are pronounced in some cases, if the herb layer is considered. Brunet et al. (2000) have shown that sharp boundaries may exist between ancient and recent forest stands, although they become more and more blurred over time. It is clear that more case studies are needed to gain a better understanding on where and why sharp and blurred boundaries emerge.

The situation becomes even more complicated if forest gaps are also taken into account (Watt, 1947). The importance of gap models (Bugmann, 2001), both in theoretical and applied forestry research (e.g. climate change effects: Price et al., 2001, near-natural forestry: Brang, 2005) is increasing rapidly. It is well known that gaps have a profound influence on environmental factors, especially on light conditions and microclimate (e.g. Chen et al., 1993; Pickett and Cadenasso, 2005; Adb Latif and Blackburn, 2010), and, consequently, on species composition and regeneration patterns (e.g. Leemans, 1990; Veblen, 1992; Fownes and Harrington, 2004; Gálhidy et al., 2006; Mihók et al., 2007; Diaci, 2008). Thus, sharp boundaries might be expected between gaps and neighbouring areas. However, this may not always be the case, especially for small gaps. The smaller the gap diameter, the more similar the gap is to areas under an intact canopy layer (Runkle, 1985).

Numerous studies have shown that the species richness of the gaps is usually higher than that of closed forests (e.g. Jonsson, 1990; Goldblum, 1997; Schnitzer and Carson, 2001; Degen et al., 2005), although the pattern is not general (e.g. Ehrenfeld, 1980). Since most studies focus on woody species, more case studies are needed that include herb species as well (Gálhidy et al., 2006). This is especially important, as herbs affect both environmental parameters and tree regeneration in gaps (Mihók et al., 2005; Gálhidy et al., 2006).

In addition, the question emerges whether boundaries of the different

vegetation layers are situated in the same positions. Some earlier studies suggest that different mechanisms are responsible for controlling the herb layer and the other layers (Tyler, 1989; Brunet et al., 2000; Holeksa, 2003; Erdős et al., 2012). Therefore, it is conceivable that boundaries of different layers are not in the same location, if the change in the main environmental factors do not coincide.

In this study, we intended to identify the spatial arrangement of forest types along a topographical gradient in a forest reserve. Our aim was to find out, whether boundaries between them are sharp or blurred. Moreover, our objective was to compare the types according to their species richness and floristic composition. We also used ecological indicator values to determine how environmental parameters change along the gradient. We hope that the present study contributes to a better understanding of the spatial heterogeneity of Central-European beech and oak forests.

2. Materials and methods

Study area

Our study area was the Kőszegi-forrás Forest Reserve (46^{0}9′ N, 18^{0}17′ E), situated in the Mecsek Mts (South Hungary), near the village of Mánfa. The reserve is located ca. 280-400 m above see level. It is among the best-studied Hungarian forest reserves (Horváth et al., 2012). Mean annual temperature is 9°C, annual precipitation is 750-800 mm (Ambrózy and Kozma, 1990). The bedrock is Miocene conglomerate, which is covered by brown forest soil. The core area of the forest reserve is 33 ha, with a buffer zone of 116.2 ha (Bartha and Esztó, 2002). Since the majority of the core area lies on a north-facing slope, the most typical plant community here is the beech forest *Helleboro odori-Fagetum*, despite the low altitude. The canopy consists of *Fagus syvatica*, although *Carpinus betulus* and *Quercus cerris* individuals are also present. The shrub layer is lacking or sparse. The cover of the herb layer varies considerably, and it has a lot of geophytes (e.g. *Allium ursinum, Galanthus nivalis, Isopyrum thalictroides*) and several plants with a sub-Mediterranean character (e.g. *Calamintha sylvatica, Lathyrus venetus, Ruscus hypoglossum*). The stand within the forest reserve is ca. 170 years old, and no forestry activities have been carried out since 1973 (Szerémy, 2008).

On the more xeric sites of the forest reserve, the turkey oak-sessile oak forest *Potentillo micranthae-Quercetum dalechampii* can be found. The canopy is formed by *Quercus petraea agg.* and *Qu. cerris*, but other species such as *Acer campestre* and *Fraxinus ornus* are also typical in the lower canopy. Both the shrub (e.g. *Cornus mas*, *Crataegus monogyna*, young individuals

of *Fraxinus ornus* and *Acer campestre*) and the herb layers (e.g. *Helleborus odorus, Melica uniflora*) are well developed. Other plant associations occurring in the forest reserve are: the alder forest *Carici pendulae-Alnetum*, the oak-hornbeam forest *Asperulo taurinae-Carpinetum* and the ravine forest *Scutellario altissimae-Aceretum*. Although these latter forest communities were not included in the present study, their species composition influences the beech forest and turkey oak-sessile oak forest of our study.

Field data collection

A 376 m × 2 m transect was established, running from a beech forest with some ravine character of the valley bottom (353 m asl) to a turkey oak-sessile oak forest on the hilltop (404 m asl). The transect consisted of 376 contiguous plots, 2 m × 1 m each. The presence of all vascular plant species of the herb layer (including trees and shrubs not higher than 50 cm) was recorded in April (to include spring geophytes) and August (to include summer plants) 2011. During field studies, boundaries of the vegetation units were determined visually, during which all vegetation layers were taken into account.

Moving split window analysis

To determine the exact and objective boundary positions along the transect, the moving split window (MSW) analysis was used (Webster and Wong, 1969). This method has proven extremely useful in vegetation science during the last few decades (Erdős et al., in press). During the MSW analysis, a window consisting of two adjacent plots is designated at one end of the transect, and the two half-windows (i.e. the two plots) are compared using a dissimilarity function. The window is then shifted along the transect, and the dissimilarity function is computed in every position. When dissimilarity function is plotted against window midpoint position, boundaries appear as peaks. The procedure can be repeated with larger window sizes, carrying out the analysis at other spatial scales. The complement of the Renkonen index was used as dissimilarity function. The significance of the boundaries was tested with the z-score transformation (Hennenberg et al., 2005). 100 randomizations were made with random relocation of plots. Z-scores were computed for all window sizes between 2-200, but finally, two spatial scales were selected for the remaining parts of the present study: z-scores were averaged over 20-30 and 40-50 window widths. Peaks above 1.85 were regarded as indicating significant ($p < 0.05$) boundaries (Erdős et al., 2013a). The MSW-computations were done using the statistical language R 2.10.1 (R Development Core Team, 2009); R-source code is published in Erdős et al. (2014).

Analysis of the segments identified along the transect

For the final boundary delineation, a combination of the MSW results and the visual boundary delineation was used. Generally, there was a good agreement between the results of the MSW for the two spatial scales; for boundary delineation, the coarse scale was used, except for the rightmost boundary (in this case, the boundary was so close to the end of the transect that it was out of reach for the coarse scale). In the case of double or multiple peaks on the MSW graph, the highest peaks were taken into account. Peaks slightly higher than the critical level (z=1.85) but not corresponding to any visual boundaries were not considered. Former studies revealed that some MSW peaks indicate within-patch inhomogeneities that may not always be important for a certain research question (Choesin and Boerner, 2002; Erdős et al., 2012). Finally, the transect was divided into eight segments, which were used for all subsequent analyses.

Species richness was calculated for all plots. To test the differences among the segments regarding species richness, one-way ANOVA and subsequent Tukey's HSD post hoc tests were made with SPSS 11.5 (SPSS Inc.). The ecological indicator values of Borhidi (1995) for temperature (T), moisture (W), soil reaction (R) and light (L) were used to estimate the environmental parameters of the segments. Several instrumental measurements have shown that ecological indicator values are appropriate to assess environmental variables (ter Braak and Gremmen, 1987; Diekmann, 1995; Barczi et al., 1997; Schaffers and Sýkora, 2000; Dzwonko, 2001; Bartha, 2002; Tölgyesi et al., 2014). We calculated mean indicator values for the plots, based on presence-absence data. The calculation of mean indicator values has a firm theoretical basis and has performed well in earlier studies (Diekmann, 2003; Lengyel et al., 2012; Tölgyesi and Körmöczi, 2012; Erdős et al., 2013b). Results were visualized in box-plots for both the species richness and the indicator values.

For each segment, the following two spectra were prepared: one using the geoelement categories (reflecting the European distribution of the plant species), and the other using the coenological preference of the species (reflecting the species' regional affinity to certain vegetation types). Categorization of the species was done following the FLÓRA database (Horváth et al., 1995).

Species names are used according to Simon (2000), plant community names follow Borhidi et al. (2012).

3. Results

Boundary delineation

In the 376 plots, a total of 65 plant species was found. Visually, eight segments were identified (G1-G3: gaps, F1-F5: forests with a canopy) (Fig. 1):

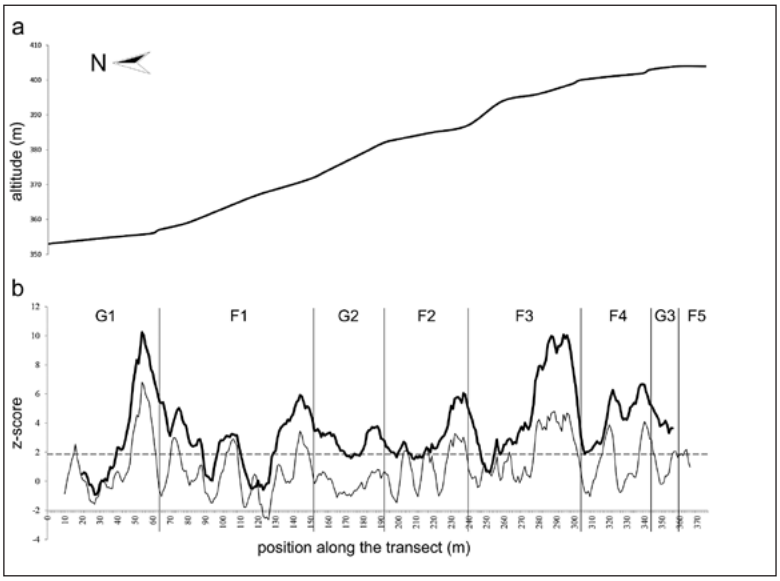

Figure 1. a) Morphological profile of the transect. b) Z-score diagram of the MSW-analysis. Vertical lines indicate visually identified boundaries. Horizontal dashed line denotes critical value (z=1.85), above which peaks are considered significant. In the MSW-analysis, z-scores were averaged over window widths 20-30 (thin line), and 40-50 (thick line).

Abbildung 1. a) Morphologisches Profil des Transekts. b) Diagramm der z-Werte von der MSW-Analyse. Senkrechte Linien zeigen visuell festgestellte Vegetationsgrenzen. MSW-Spitzen über der waagerechten gestrichelten Linie (kritische Wert, z=1.85) sind signifikant. Mittelwerte von den z-Werten wurden berechnet zwischen Fenstergrössen 20-30 (dünne Linie) und 40-50 (dicke Linie).

G1: The transect started from a gap, characterized by a relatively dense shrub layer (e.g. *Sambucus nigra*), and a large amount of tree saplings (mainly *Fagus sylvatica*). The cover of the herb layer usually varied between 30-60%, the most abundant plants being *Dentaria bulbifera*, *Dryopteris filix-mas*, *Galeobdolon montanum* and *Rubus fruticosus agg*.

F1: The second segment was a forest with a canopy dominated by *Fagus sylvatica*. Tree saplings formed a lower canopy layer. The shrub layer was almost entirely lacking. The herb layer was sparse, the most abundant species included *Dentaria bulbifera*, *D. enneaphyllos* and *Ranunculus ficaria*.

G2: The third segment was a gap with a considerable shrub layer, formed mainly by juvenile *Fagus sylvatica* trees. *Dentaria enneaphyllos, Galeobdolon montanum, Melica uniflora* and *Mercurialis perennis* were dominating in the herb layer, total cover of which was usually over 60%.

F2: This segment had a relatively open canopy, resulting in a considerable shrub layer (*Euonymus europaeus* and *juvenile Fagus sylvatica* individuals). The cover of the herb layer varied considerably from plot to plot, and it was co-dominated by *Dentaria enneaphyllo*s and *Ranunculus ficaria*.

F3: A pure stand of mature *Fagus sylvatica* trees formed a dense canopy, which resulted in a sparse shrub layer. Moss-covered rocky outcrops were frequent. The cover of the herb layer varied extremely, its abundant species being *Dentaria enneaphyllos* and *Mercurialis perennis*.

F4: Compared to the previous segments, this segment was quite different regarding species composition. In the canopy, *Quercus cerris* was the dominant species, with *Acer campestre* and *Fraxinus ornus* in the lower canopy layer. The shrub layer consisted mainly of *Cornus mas* and *Crataegus monogyna*. A few large rocks were on the soil surface. In the herb layer, *Dentaria bulbifera*, *Mercurialis perennis* and *Ranunculus ficaria* had the highest cover values.

G3: The shrub layer of this gap consisted mainly of *Cornus mas* and *Crataegus monogyna*. Among seedlings and saplings, *Acer campestre* was especially frequent. Along the whole transect, the cover of the herb layer was the highest in this segment, co-dominated by *Melica uniflora* and *Mercurialis perennis*.

F5: The transect ended in a rather xeric forest, canopy of which was formed mostly by *Quercus cerris*, but several other trees were also present (e.g. *Acer campestre, Carpinus betulus, Fraxinus ornus, Qu. petraea agg.*). The open canopy enables the existence of a dense and diverse shrub layer (*Cornus mas, Crataegus monogyna, Euonymus europaeus, Rosa canina agg.*). Also, the cover values of the herb layer were the second highest in this segment.

The segments identified visually were generally confirmed by the MSW analysis (Fig. 1). Each of the seven visual boundaries was indicated by a corre-

sponding peak on the MSW profile. Most of the peaks were prominent. A few additional peaks also emerged. Although these additional peaks may refer to important compositional changes, which could be further analyzed, they were not considered in the present study. From the MSW profile, it is apparent that the MSW peaks were shifted to the north in each case, compared to the visual boundaries. The spatial difference was 3-10 m, with an average of 6.14 m.

Analysis of the segments

Species number differed significantly among the segments along the gradient (ANOVA $F=37$, $p<0.001$). Tukey's post hoc comparisons showed that forest gaps (G1-G3) and section F5 were more species-rich than the other segments (Fig. 2).

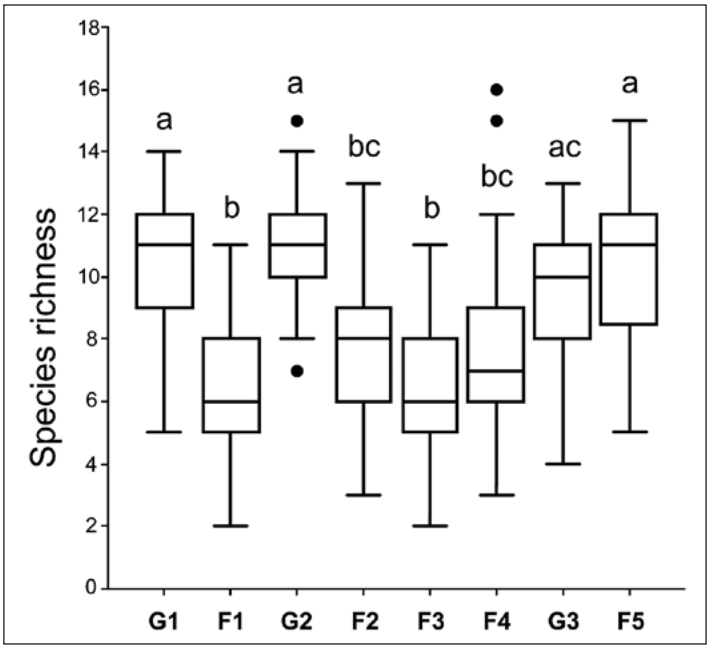

Figure 2. Species richness of the segments along the gradient. Boxes not sharing a letter are significantly ($p<0.001$) different.

Abbildung 2. Artenreichtum der Abschnitten entlang des Gradienten. Unterschiedliche Buchstaben kennzeichnen signifikante ($p<0.001$) Unterschiede.

Mean temperature values were low near the valley bottom, slightly higher in segments F2 and F3, intermediate in segment F4, and reached the highest values on the edge of the valley (Fig. 3a). Mean moisture values showed a reverse trend, with the exception of segment F1, which seemed to be somewhat dryer than the neighbouring segments (Fig. 3b). As for the soil reaction values, the whole transect was dominated by plants indicating neutral soils or having a wide tolerance (category R6), and by slightly basifrequent species (category R7). However, soil reaction values increased near the middle of the transect (Fig. 3c). Mean light values were relatively high in segments F4, G3 and F5 (Fig. 3d). Among the other segments, the largest gap (G1) seemed to have a bit higher values.

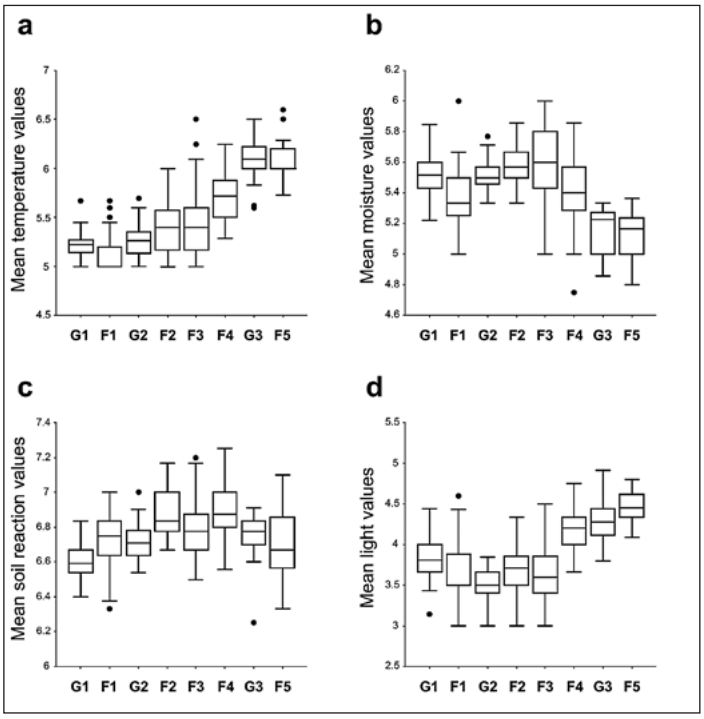

Figure 3. Mean ecological indicator values of the segments along the gradient. a) mean temperature values, b) mean moisture values, c) mean soil reaction values, d) mean light values.

Abbildung 3. Durchschnittliche Zeigerwerte in den Abschnitten entlang des Gradienten. a) Temperatur, b) Feuchtigkeit, c) Bodenreaktion, d) Licht.

Regarding the geoelement spectra, the whole transect was dominated by European, Central European and Eurasian species (Fig. 4). The proportion of the sub-Mediterranean species increased considerably towards the edge of the valley. Also, species with a continental character showed a slight increase in the same direction. Atlantic and cosmopolitan species played a subordinated role.

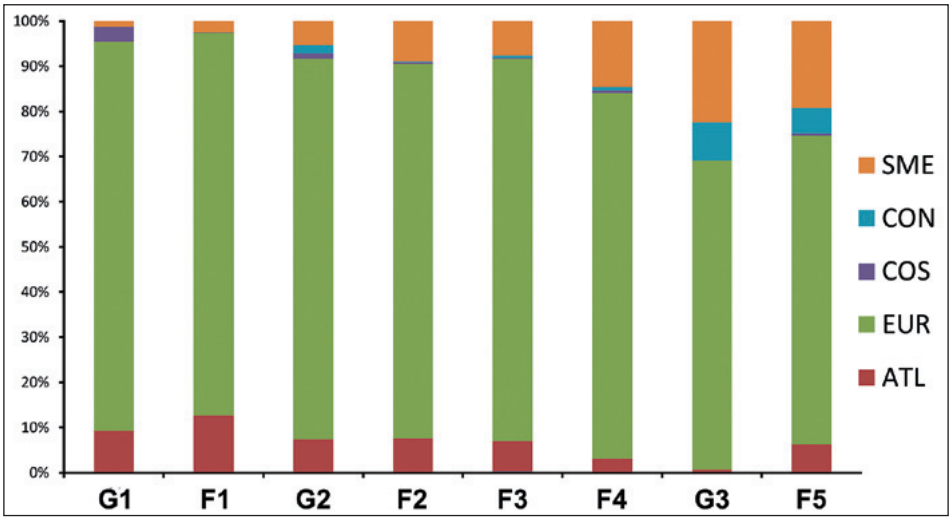

Figure 4. Geoelement spectra of the segments along the gradient. SME: sub-Mediterranean species, CON: continental species, COS: cosmopolitan species, EUR: European, Central-European and Eurasian species, ATL: Atlantic species.

Abbildung 4. Spektrum der Florenelementen in den Abschnitten entlang des Gradienten. SME: submediterrane Pflanzen, CON: kontinentale Pflanzen, COS, Kosmopoliten, EUR, europäische, zentral europäische und eurasische Pflanzen, ATL: atlantische Pflanzen.

If the coenological preferences of the species were considered, there was a conspicuous trend from the valley bottom to the valley edge (Fig. 5): the proportion of beech forest species gradually decreased, while species of xeric and mesic oak forests became more frequent. Weedy and indifferent species were rare throughout the whole transect.

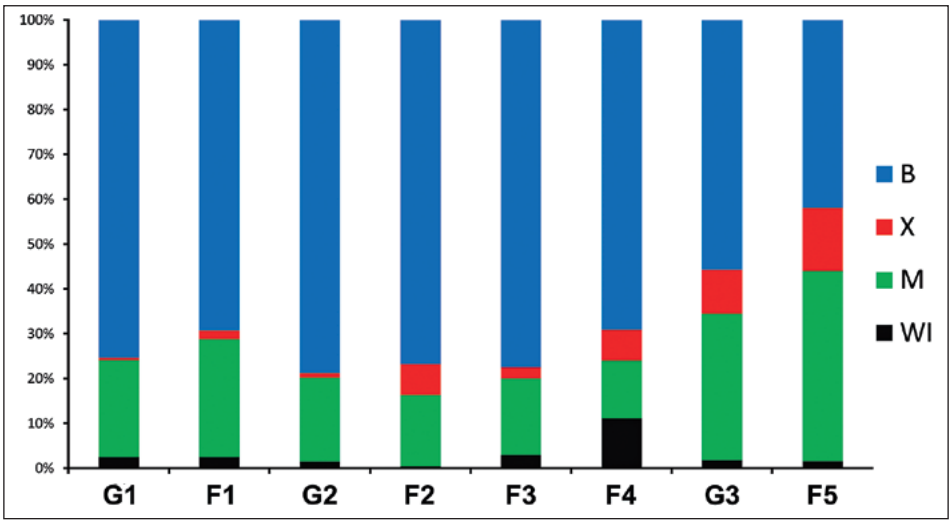

Figure 5. Coenological preference spectra of the segments along the gradient. B: beech forest species, X: xeric oak forest species, M: mesic oak forest species, WI: weedy and indifferent species.

Abbildung 5. Spektrum der zönologischen Präferenzen in den Abschnitten entlang des Gradienten. B: Arten der Buchenwälder, X: Arten der xerophilen Wälder, M: Arten der mesophilen Wälder, WI: Unkräuter und indifferente Arten.

4. Discussion

It is generally accepted that natural forests consist of a mosaic of patches in different developmental stages (the so-called sylvatic mosaic: Oldeman, 1990; Valverde and Silvertown, 1997), or growing under different site circumstances and dominated by different plant species (Wall and Darwin, 1999; Perry et al., 2008). The aim of our study was to characterize the heterogeneity of the herb layer in a forest reserve along a topographical gradient.

Our results clearly indicated that the MSW technique is able to detect boundaries between different forest types. As expected, there were sharp boundaries between gaps and forests with a closed canopy. In addition, prominent peaks emerged between the segments F2, F3 and F4 (Fig. 1). Our results are in good agreement with those of Brunet et al. (2000), Pärn et al. (2010) and Bátori et al. (2014), who also found well-defined boundaries between different forest-types. In all these cases, the neighbouring communities were situated along marked gradients: different past land-use methods

(Brunet et al., 2000), strongly different soils (Pärn et al., 2010) or steep topographical slopes (Bátori et al., 2014). The study of Tang and Ohsawa (2002) also indicates that conspicuous environmental gradients may result in sharp boundaries, although this latter study included only woody species. On the other hand, some studies showed gradual changes in species composition along transects crossing two or more forest communities (Penksza et al., 1995; Ortmann-Ajkai, 2002; Erdős et al., 2012, 2013a). In these latter cases, environmental parameters did not vary as much along the transect, resulting in a rather gradual, continuous species turnover. Similarly, in grassland communities, it has been shown that steep environmental gradients often entail sharp vegetation boundaries, while gradual environmental changes result in gradual compositional changes (Werger et al., 1983; Zalatnai and Körmöczi, 2004). However, it should be kept in mind that sharp vegetation boundaries might emerge even in the absence of environmental boundaries, due to non-linear species responses (Fagan et al., 2003). Therefore, we have to emphasize that more case studies will be needed to draw firm conclusions valid for forests.

Unfortunately, the detection of the boundary between segments G3 and F5 was rather uncertain. This boundary was so close to the end of the transect that the coarse scale could not be used in the MSW analysis. The graph of the fine scale showed significant but not very high peaks.

We found that boundaries identified by the MSW were always shifted to the north, when compared to visual boundaries (Fig. 1). The possible explanation for this can be given as follows. Visual boundaries were determined based on all vegetation layers, including shrubs and canopy trees. In contrast, MSW-boundaries were delineated using only the data of the herb layer. For herb species, the most important factor affecting their distribution is microclimate, mainly light regime (e.g. Tinya et al., 2009a, b). Microclimatic parameters are largely influenced by the canopy layer. Since the surface is receiving solar radiation from a prevailingly southern direction, this causes that canopy closure (shading) is reflected in the herb layer a few meters towards the north. The effect is especially explicit in the present study, given the north-facing character of our transect. The pattern revealed in our study is consistent with the results of light intensity measurements of Gálhidy et al. (2006), Diaci et al. (2008) and Kollár (2013).

We revealed significant differences between the species richness of the segments (Fig. 2). Generally, gaps seemed to be more species rich than other areas. This finding corresponds to the results of earlier studies, carried out in several forest types (e.g. Jonsson, 1990; Goldblum, 1997; Schnitzer and Carson, 2001; Degen et al., 2005; Böhling, 2007). The present article empha-

sizes the importance of the gaps in maintaining a high diversity of Hungarian beech and oak forests.

While in the case of species richness, the main difference was found between gaps and closed forests, this was not true for the ecological indicator values. Mean temperature, moisture, soil reaction and light values were primarily influenced by the position along the topographical gradient. Conditions near the valley bottom were cool, humid and shady, whereas the factors changed towards the other end of the transect. The valley edge proved to be rather warm, xeric, and sunny. Although it is certain that parameters differ among gaps and closed forests, it seems that in our case, the strong topographical gradient had a much larger influence on environmental factors than canopy openness. In addition, it must be taken into account that segments F4 and F5, although categorized as closed forests, had a much more open canopy than segments F1-F3. Clearly, it should always be kept in mind that gap vs. non-gap dichotomy, although a useful distinction for practical purposes, is an oversimplification (Lieberman et al., 1989). It is probable that the small gap sizes also minimized environmental differences. Lateral extension of the trees bordering the gap as well as growing saplings are able to create an environment similar to those under the closed canopy, especially in the case of small gaps (Runkle, 1985).

Geoelement types also reacted mainly to the climatic conditions caused by the topographical gradient: the frequency of the sub-Mediterranean and continental species increased slightly towards the hilltop (Fig. 4). Coenological preferences showed a similar trend: species typical of xeric and mesic forests were more frequent near the hilltop, while plants of beech forests were most numerous in the lower and middle section of the transect (Fig. 5). The low frequency of weedy and indifferent species along the whole transect indicates the good natural condition of the core area of the forest reserve.

Knowledge on the dynamic processes of natural forests is important both from a theoretical and a practical perspective (Brang, 2005; Kenderes et al., 2008). Our study may serve as a useful starting point for further monitoring surveys. Such surveys could considerably contribute to our understanding of how gap-forest boundaries change over time.

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